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Reevaluation of the taxonomic status of North African gerbils usually referred to as *Gerbillus pyramidum* (Gerbillinae, Rodentia): Chromosomal and biometrical data

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Abstract

The chromosomal and biometrical attributes of large-sized, hairy-footed gerbils from North Africa usually referred to as *Gerbillus pyramidum* were studied. High-resolution banding techniques as well as external and skull biometry were used to compare specimens from Mauritania and Algeria. All specimens studied were characterized by the same karyotype, comprising 40 chromosomes and 74 autosomal arms. Gerbils from Algeria were found to be larger than those from Mauritania for most of the skull measurements, as well as for some external measurements. Comparisons with published data from other North African countries (Senegal, Morocco, Tunisia) suggest that all the previously figured 2 n = 40 karyotypes do represent the same species, chromosomally significantly distinct from 2 n = 38 chromosome individuals found in Egypt and Sudan that correspond to true *Gerbillus pyramidum*. Based on our results and awaiting contrary evidence, we propose that the 2 n = 40 chromosome specimens found from Senegal to Libya correspond to a unique species, for which the name *Gerbillus tarabuli* should be applied. This species of wide distribution in northern Africa shows an apparently important biometrical variability, to be related with eco-climatological variations of the environment in which these populations live.

Key words: *Gerbillus*, North Africa, chromosomes, biometry, systematics

Introduction

Rodents of the genus *Gerbillus* constitute a significant part of the arid and semiarid communities of mammals, from North Africa to India through the Arabian Peninsula and the Middle East. From a taxonomic point of view, their diversity is established, but, as stated by Musser and Carleton (1993), ... "[t]his genus has never been adequately revised". As a result, the number of species recognized has varied considerably according to various authors (see review in Lay 1983), until Lay (1983) produced a list of 62 tentative species which was nearly entirely adopted by Musser and Carleton (1993). Clearly identified in these lists, a number of taxonomic questions remained. Part of this problem undoubtly lies in the great number of ancient, often superficial, descriptions of new taxa that were only based on crude comparisons of colour and other morphological (external and a few skull) characteristics. The use of new morphological characters (see Lay 1983) and, more importantly, the development of cytogenetical investigations (starting from Matthey 1952) have improved our knowledge of the systematics in this group, without providing, however, significant clarification in its taxonomic arrangement to date.

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Among the taxonomical problems identified in *Gerbillus*, the status of large-sized, hairy-footed gerbils from North Africa, the Sinai, and Israel that have been referred to as *Gerbillus pyramidum* Geoffroy, 1825 is still a matter of debate. Often considered to include populations of individuals characterized by diploid numbers of chromosomes (2 n) ranging from 38 (Wassif et al. 1969) to 66 (Wahrman and Zahavi 1955), the name *G. pyramidum* was restricted by Lay (1983, following Lay et al. 1975) to 2 n = 38 specimens from Egypt and Sudan. According to the latter author, the populations from the Sinai and coastal areas of Israel characterized by high diploid numbers should be referred to a species yet to be identified, but probably different from *G. pyramidum*. On the other hand, populations from North Africa west of Egypt and Sudan have been studied by various authors, under different species names. When performed, standard chromosomal analyses regularly yielded 2 n = 40 chromosomes for individuals from these populations: Tunisia (Jordan et al. 1974; Chibani and Lamine-Cheniti 1982), Morocco (Lay et al. 1975), Algeria (Matthey 1952), Mauritania (Klein et al. 1975), Senegal (Hubert and Böhme 1978; Granjon et al. 1992). In this region, two species have been described, which are proposed by Lay (1983) as potentially valid, and possibly characterized by this diploid number of 40 chromosomes. These are *G. tarabuli* described by Thomas (1902) from Libya (initially as a subspecies of *G. pyramidum*), and *G. riggenbachi*, described by the same author (Thomas 1903) from Western Sahara (and then said to be ... "[a] representative of *G. pyramidum*").

In this study, we investigate gerbils from Mauritania and Algeria using high resolution chromosome banding techniques, and also bring together all the available biometrical information (including original one) on these large-sized gerbils from North Africa, with the aim of discussing the systematic implications of these data, and making some suggestions about the nomenclature in this group.

Material and methods

The skulls and skins of the specimens studied are deposited in the collection of the Laboratoire de Zoologie, Mammifères et Oiseaux, at the Museum National d'Histoire Naturelle. The tissue explants and a portion of the cells of the karyotyped specimens are routinely kept in liquid nitrogen in the cell and tissue collection of the same laboratory.

Chromosomal analyses

Six specimens (3 females and 3 males) of large-sized, hairy-footed gerbils from coastal areas of Mauritania, as well as two specimens (one female and one male) from Béni Abbès (Algeria) have been karyotyped. Chromosome analysis was performed on preparations obtained from fibroblast cultures established after tail biopsy. Mitotic chromosomes were studied by G-banding (GTG; Seabright 1971), R-banding (RBG; Viegas-Pequignot and Dutrillaux 1978) and C-banding (CBG; Sumner 1972; see ISCN 1995). For each specimen, at least 20 metaphases were analysed. The origin, sex, and number of the specimens studied are as follows: Mauritania: from Ivik, Banc d'Arguin (male n° 88–006); near Nouamghar (female n° 95–002; male n° 95–007); surroundings of Nouakchott (male n° 95–035; female n° 95–081); Tamzakt (male n° 95–082). Algeria: from Béni-Abbès (male n° 97–013; female n° 97–044).

Morphometric analyses

Preliminary analyses have revealed the presence of at least 4 species of *Gerbillus* in coastal areas of Mauritania (Granjon et al. 1997). Among them, a sample of 27 adult specimens of large-sized, hairy-footed gerbils referable to the species with 2 n = 40 chromosomes has been isolated, on the basis of the confrontation of cytogenetical, morphological, and biometrical results (unpubl. data). The sample from Algeria is composed of 15 adult specimens from Béni Abbès and El Goléa. On all these specimens, classical external measurements (weight, head and body, tail, hind foot, and ear length) have been taken, as well as 8 skull measurements: GLS (greatest length of skull), ZYW (greatest zygomatic width), IOB (least

breadth of interorbital constriction), DIA (length of diastema), LPF (length of palatal foramina), UTR (crown length of upper tooth row), BBC (breadth of braincase) and BUL (greatest length of bullae). These measurements have been taken as described in Chimimba and Dippenaar (1995). They were selected for comparative purpose with other studies, being the more regularly presented measurements on *Gerbillus* skulls. The origin, sex, and number of the specimens studied are as follows: Mauritania: from the surroundings of Nouakchott, Trarza (females n° 1994.1273 and 1997.1495, male n° 1994.1272); from Nbeika, Tagant (male n° 1997.1479); from Agneitir, Inchiri (female n° 1997.1481); from Sei-Rakna, Trarza (females n° 1997.1484 and BLM386, male n° BLM388); from Amatlich El Gleitat, Adrar (male n° 1997.1480); from Tiguent, Trarza (female n° 1997.1486, males n° 1997.1485, and BLM391); from Tamzakt, Trarza (female n° 1997.1494, males n° 1997.1482, 1997.1483, 1997.1491, BLM448, and BLM455); from Chott Boul, Trarza (females n° 1997.1490, 1997.1496, 1997.1497, BLM441, and BLM459A, male n° 1997.1489); from Akchar, Inchiri (female n° 1997.1474, male n° BLM423); from Hassi Tifouggag, Brakna (male n° 1997.1493). Algeria: from El Goléa (females n° 1997.503, 1997.504, 1997.505, and 1997.506, males n° 1997.507 and 1997.508); from the surroundings of Beni-Abbès (males n° 1997.509, 1997.510, 1997.511, 1997.513, 1997.514, 1997.515, and 1997.516, females n° 1997.512 and 1997.517).

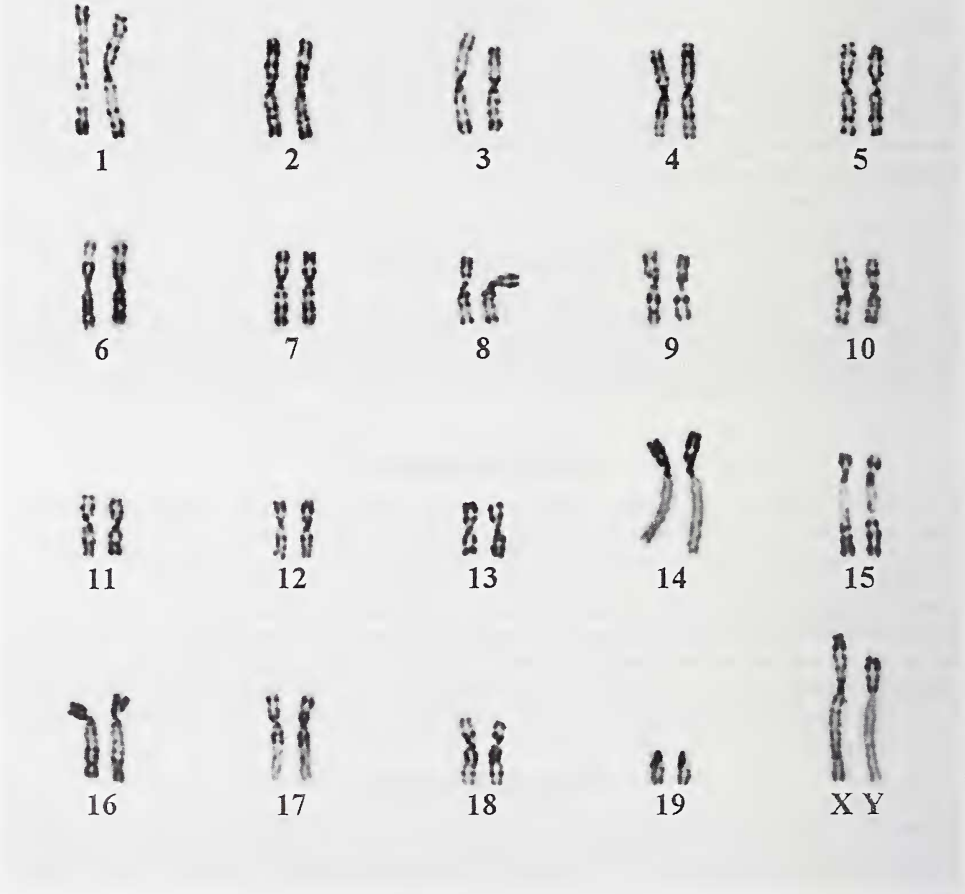

Fig. 1. R-banded (RBG) karyotype of a male *G. tarabuli*. Note that in addition to the late replicating long arm of the Y chromosome, the long arm of pair 14, an intercalar segment of the long arm of pair 1 and distal segments of the pairs 17 and 18 are also late replicating.

Results

Chromosomal analysis

After R-banding, the karyotypes of the six specimens from Mauritania and the two specimens from Algeria were found to be identical. They consist of 40 chromosomes comprising 13 pairs of metacentric, 5 pairs of submeta- to subtelocentric and one pair of acrocentric chromosomes, resulting in a number of autosomal arms (NFa) of 74. Both sex chromosomes are large submetacentrics, the X chromosome being the largest of the set and the Y chromosome being equal in size to the second pair of autosomes. Their short arms are identical and result from an autosome-gonosome translocation (Fig. 1). In spite of the important quantity of C heterochromatin revealed in all centromeric and some intercalar regions (Fig. 2), no well-defined heteromorphism for C-band positive heterochromatin was observed.

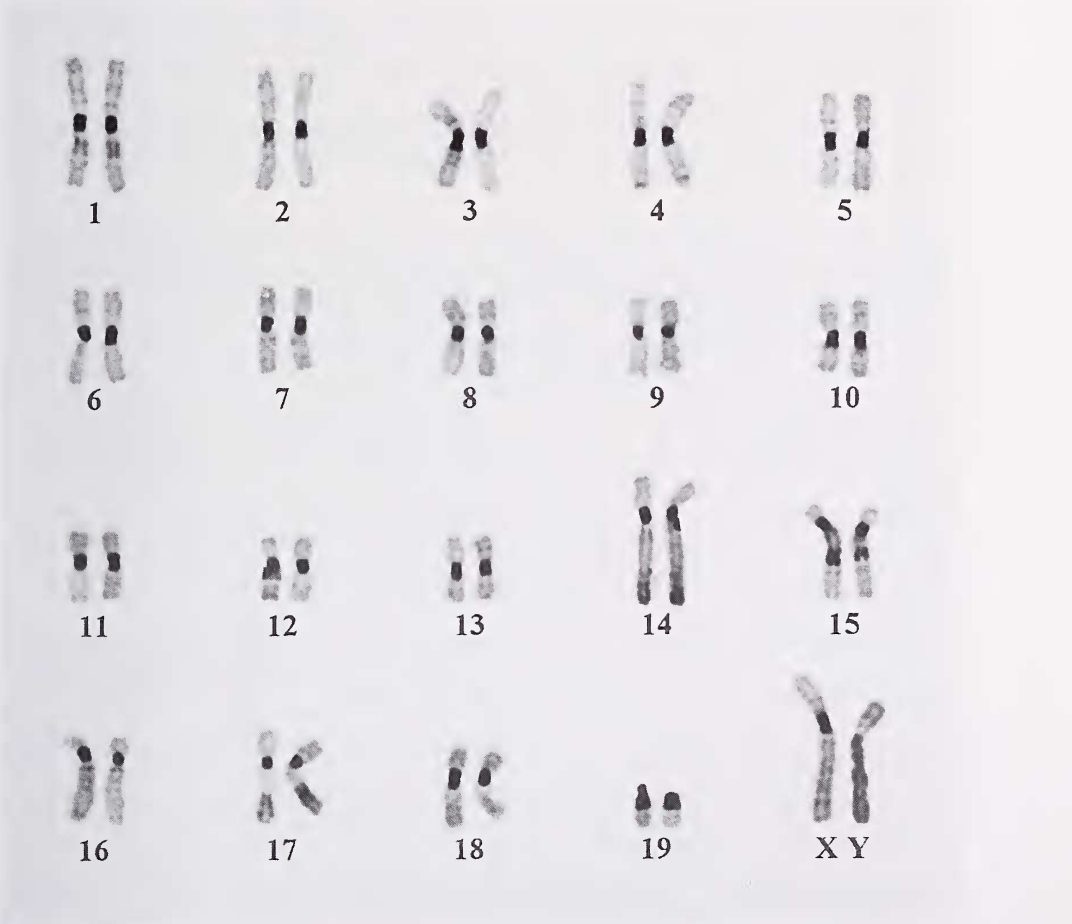

Fig. 2. C-banded (CBG) karyotype of male *G. tarabuli*. Note that the late replicating segments of the Fig. 1 are C-band positive.

Morphometric data

The ranges of variation of the measurements taken on the samples from Mauritania and Algeria are given in tables 1 (body measurements) and 2 (skull measurements), together with the values extracted from various other studies. No statistical test could be performed between our data and those from other authors, due to the fact that individual data (and/or standard deviation values) were rarely available in the latter. Between the series of Algeria and Mauritania that we measured, significant differences were found for all skull measurements, except diastema length (Mann-Whitney U tests, $p < 0.05$), the specimens from Algeria being consistently larger. As far as body measurements are concerned, Algerian specimens were found to be larger for hindfoot (U test, $p = 0.0003$) and weight (U test, $p = 0.014$) values, whereas Mauritanian specimens were found to be larger for tail length (U test, $p = 0.0001$) and ear length ($p = 0.0314$) values.

For Mauritania, our data mostly fall in the range of the values given by Klein et al. (1975) for a sample of *Gerbillus* sp. "*agag* group" characterized by a 40 chromosome karyotype. However, our sample appears characterized by a somewhat longer tail and, possibly, a longer hindfoot (but Klein et al. [1975] did not indicate precisely whether they included the claw in their measurement). Concerning the Algerian specimens, our results also correspond to the range of variation indicated by Kowalski and Rzebik-Kowalska (1991), the latter being so large that one may suspect that young individuals were included in the sample considered by these authors.

For all these measurements, the sample of *G. pyramidum* from Egypt (Osborn and Helmy 1980) reaches the highest values, the specimens of *G. p. pyramidum* from the Nile Valley being the largest of all.

Table 1. Body measurements (in mm) of samples of large-sized, hairy-footed gerbils from Northern and Saharo-Sahelian Africa, often referred to as *G. pyramidum*. TL = Total length; HB = Head and body length; Hf = Hindfoot length; E = Ear length. The sample from Egypt includes *G. p. pyramidum*, *G. p. gedeedus* and *G. p. elbaensis*.

	TL	HB	T	Hf	E	Reference
G. p. tarabuli type		105	149	30 (s. u.)	15	Thomas (1902)
G. riggenbachi type		101	132	30 (s. u.)	13	Thomas (1903)
G. pyramidum Senegal (n = 1)		122	156	34	14	Hubert and Böhme (1978)
Gerbillus sp. ("agag" group) Mauritania (n = 46)		91–117	123–148	26–29	12–16	Klein et al. (1975)
Gerbillus sp. Mauritania (n = 27)		89–108	134–161	27–31	13–16	This study
G. pyramidum Algeria (n = 83–87)	200–274		110–172	25–32	13–17.5	Kowalski and Rzebik-Kowalska (1991)
Gerbillus sp. Algeria (n = 14)		80–110	130–150	28–35	12–15	This study
G. pyramidum Tunisia (n = 30)	222–267		124–149	27–35	13–17	Jordan et al. (1974)
G. p. tarabuli Lybie (n = 31)	246–289		132–165	30–35	14–17	Ranck (1968)
G. p. tibesti Tchad (n = 15)	258–300		146–176	32–37	15–18	Setzer and Ranck (1971)
G. pyramidum, Egypte (n = 60–70)		102–135	128–180	30.5–39	14–20	Osborn and Helmy (1980)
G. pyramidum, Sudan (n = 5)		97–121	125–149	28.3–30	11.9–16.1	Tawill and Niethammer (1989)

Table. 2. Skull measurements (in mm) of samples of large-sized, hairy-footed gerbils from Northern and Saharo-Sahelian Africa, often referred to as *G. pyramidum*. See text for abbreviations, explanation, and table 1 for references.

	ONL	CBL	ZW	NL	IOB	D	PFL	UMR	BCW	B
G. tarabuli type	32.7	25	17.2	13	6.6	9	6	4		
G. riggenbachi type	31	33 (sic)	16.2	12	6.5	8.5		4	14	10.2
G. pyramidum Senegal (n = 1)	34.8		19.1		6.1			4.8		9.3
Gerbillus sp. ("agag" group) Mauritania (n = 46)	28.6–32.4							3.5–4.3		
Gerbillus sp. Mauritania (n = 27)	29.4–31.7	26.3–20.0	15.7–17.5		5.6–6.3	7.5–8.9	4.7–5.6	3.5–4.2	13.6–14.4	8.6–9.9
G. pyramidum Algeria (n = 83–87)		24.8–31.2	14.8–18.2		5.3–7.0			3.9–4.9		
Gerbillus sp. Algeria (n = 10–12)	30.8–34.7	27.2–31.3	16.5–18.7		5.9–6.7	7.6–9.1	4.9–5.8	4.1–4.5	13.7–15.0	9.5–10,6
G. pyramidum Tunisia (n = 30)	29.5–34.5	25.9–30.9	15.6–19.0		5.7–6.9		3.8–4.8	4.4–5.9	14.1–15.4	10.2–12.6
G. pyramidum tarabuli Lybia (n = 31)	31.8–35.6		16.7–18.6	12.4–14.3	6.3–7.4			3.9–4.5		11.2–12.3
G. p. tibesti Tchad (n = 15)	31.5–35.2		16.7–18.7	12.4–14.6	5.9–7.1			3.8–4.3		11.5–12.7
G. pyramidum, Egypte (n = 60–73)	32.5–38.1		16.8–20.8	12.5–15.5	6.0–7.4		5.2–6.4	4.5–5.5	14.5–16.3	9.2–11.5
G. pyramidum, Sudan (n = 4)	31.2–34.4	26.8–33.7	16.6–17.6				5.3–6.0		15.0–16.0	

Discussion

A karyotype with 2n = 40, NFa = 74, comprising 18 pairs of submetacentric to metacentric and one small pair of acrocentric autosomes has already been presented for large-sized, hairy-footed gerbils from Senegal (Hubert and Böhme 1978; Granjon et al. 1992), Morocco (Lay et al. 1975), and Tunisia (Jordan et al. 1974; Chibani and Lamine-Cheniti 1982). Earlier drawings of the chromosomes of Algerian specimens by Matthey (1952) are more difficult to interpret, but most probably represent the same pattern. The X chromosome appears as a relatively large submetacentric and the Y chromosome as a middle sized submetacentric in Lay et al. (1975), whereas both sex chromosomes appear as metacentrics slightly different in size in Jordan et al. (1974). In all instances, two relatively large pairs of submetacentric chromosomes characterized by very small short arms are clearly visible, but the number of other pairs identified as submetacentrics varies from 5 (Jordan et al. 1974) to 9 (Lay et al. 1975). However, the absence of chromosome banding in these studies makes it difficult and somewhat arbitrary to identify chromosome morphology unambiguously (metacentric vs submetacentric, or submetacentric vs subtelocentric). Slightly different arrangements and interpretations of these karyotypes can be done, resulting in figures very similar to the ones we obtained in the specimens from Mauritania and Algeria that we studied. Awaiting further data, these similarities suggest a more or less complete homology between the 2n = 40 karyotypes reported from all these countries, a fact that was proven here between the specimens from Mauritania and Algeria by virtue of high resolution banding techniques.

On the other hand, the karyotype of specimens from Egypt as shown in Wassif et al. (1969) and Lay et al. (1975) is characterized by 38, all meta- to submetacentric chromosomes. Four pairs are considered to be submetacentric by Lay et al. (1975), among which not one appears to have particularly short arms. The same may be true in the specimens from Sudan studied by Tawil and Niethammer (1989), who described the chromosomes to be all metacentric or submetacentric, but no photograph of the karyotype was provided in this study. Moreover, many other chromosomes are clearly distinct in size and morphology from those figured in karyotypes with 2n = 40. This means that at least some of them are rearranged differently between the two karyotypes (2n = 38 and 2n = 40). For instance, the absence of acrocentric pairs in 2n = 38 chromosome gerbils is most probably the result of a tandem translocation, a chromosomal rearrangement known for its strongly negative heterotic effect in the heterozygous state (Wright 1982). Finally, the comparison of G-, R- and C-banded sex chromosomes of *G. pyramidum* (see Fig. 2 in Wahrman et al. 1983, where unfortunately chromosome banding data were not presented for autosomes) with those of the 2n = 40 individuals presented here, shows clear differences.

It appears finally that there is probably more than a simple difference of one pair of small acrocentric chromosomes (that could be explained by one single event) between the 2n = 38 and 2n = 40 karyotypes. This difference needs to be more accurately documented, which will be possible once 2n = 38 specimens are studied by high resolution banding techniques. Nevertheless, the rearrangements suggested by the comparison made above constitute a strong argument for considering the specimens characterized by these two karyotypes as belonging to two distinct species. The eastern, 2n = 38, one corresponds to *G. pyramidum*, the type specimen of which was collected in the surroundings of the Great Pyramids in Egypt, and which would range along the Nile Valley, in Egypt, and Sudan, and in the oases of the region as proposed by Musser and Carleton (1993). On the other hand, the apparent homogeneity of the 2n = 40 chromosome karyotype from Northern Senegal in the West eastwards to Tunisia suggests that the corresponding specimens may belong to only one species. *G. riggenbachi* was described by Thomas (1903) from Rio de Oro, a coastal site on the Tropic of Cancer which is some 350–400 km distant

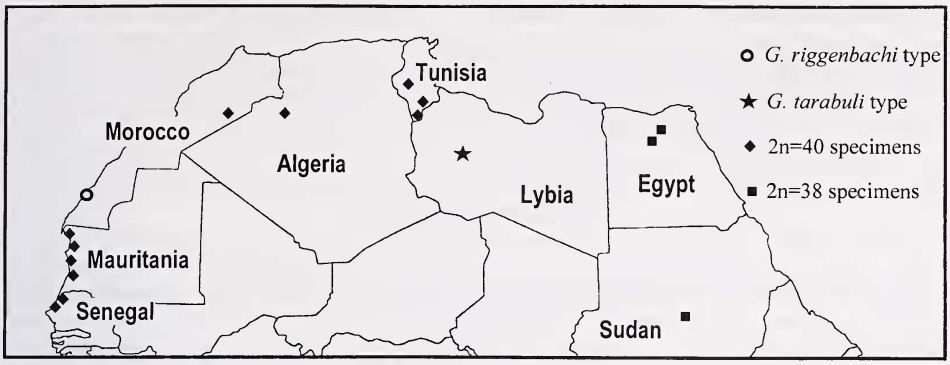

Fig. 3. Map of northern Africa, showing localities where 2 n = 40 and 2 n = 38 chromosome specimens of *Gerbillus* have been recorded, and type-localities of *G. riggenbachi* and *G. tarabuli*.

from the site where the specimens from Northern Mauritania chromosomally analysed here originated (Fig. 3). *G. pyramidum tarabuli* was described by the same author one year earlier, on the basis of specimens caught in various localities of central West and the coastal North of Libya (Thomas 1902). A number of these localities, including Sebha, from which the type specimen was caught, are situated 550 to 600 km east from south-eastern Tunisia (Fort Saint), where Jordan et al. (1974) reported specimens with 40 chromosomes (Fig. 3). Although the whole region can be environmentally subdivided in a number of ways (see, for instance the climatic and phytogeographic subdivisions presented by Le Houerou (1992), an arid to semi-arid nucleus has persisted at least throughout the Pleistocene and Holocene in the lowlands along the Tropic of Cancer, which extension has varied according to climatic changes (Le Houerou 1992). The absence of a significant north-south barrier between the western coast and the Libyan desert is another argument to support the existence of one wide-ranging species of large-sized, hairy-footed gerbil characterized by the 2 n = 40, NFa = 74 karyotype described here. Contrary to Lay (1983, followed by Musser and Carleton 1993), we thus propose to abandon *G. riggenbachi* as a valid species and, for reasons of priority, to consider only *G. tarabuli* as being present in this region. Its distribution would range, more or less continuously, from northern Senegal in the west (Duplantier et al. 1991) to the Cyrenaican Plateau of Libya (Ranck 1968) and the Tibesti Mountains of Chad (Setzer and Ranck 1971) in the east. The hiatus in *G. pyramidum* distribution mentioned by Ranck (1968) in eastern Libya and western Egypt, corresponding to the Cyrenaican Plateau and the northern part of the Libyan desert may well represent the barrier that has been at the origin of the differentiation between *G. pyramidum* and *G. tarabuli*.

The morphological and biometrical data appear of relatively little value for a priori characterization of these species. Specimens of *G. pyramidum* from Egypt can reach a larger size than that of specimens from the other origins but the biometrical characteristics of the series from Sudan fall in the range of the values obtained for other samples. Conversely, significant differences can be evidenced between samples of *G. tarabuli* from various origins (as here between the samples from Mauritania and Algeria). This apparently important morphometrical variability within both *G. pyramidum* and *G. tarabuli* is probably related to eco-climatological variations of the environment in which these populations live (see Petter 1961), and would deserve further analyses. The proposal of Lay et al. (1975) to consider *G. riggenbachi* as a distinct species, following comparison of museum specimens, has never been substantiated, and would need to be critically examined on the basis of large-scale analyses, taking into account this environmentally and geo-

graphically determined variability. Meanwhile, it seems important to gather as much chromosomal information as possible on these gerbils from all over North Africa, in an attempt to map more precisely their distribution. The establishment of diagnostic morphological characteristics could then be envisaged, to determine whether splitting of what we propose to call *G. tarabuli* is justified.

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Zusammenfassung

Neubewertung der taxonomischen Stellung nordafrikanischer Rennmäuse, die gewöhnlich Gerbillus pyramidum (Gerbillinae, Rodentia) zugeschrieben werden: Chromosomale und biometrische Daten

Es wurden die chromosomalen und biometrischen Characteristika großer, nordafrikanischer Rennmäuse untersucht, die gewöhnlich dem Taxon *Gerbillus pyramidum* zugeschrieben werden. Hochauflösende Bänderungstechniken zur Chromosomenanalyse wie auch verschiedene Körper- und Schädelmaße wurden zum Vergleich von Tieren aus Mauretanien und Algerien herangezogen. Alle untersuchten Rennmäuse zeigten den gleichen, durch 40 Chromosomen und 74 autosomale Arme gekennzeichneten Karyotyp. Rennmäuse aus Algerien waren generell größer als jene aus Mauritanien. Vergleiche mit den publizierten Angaben über Rennmäuse aus anderen nordafrikanischen Ländern (Senegal, Marokko, Tunesien) legen nahe, daß alle zuvor beschriebenen 2 n = 40 Karyotypen dieselbe Spezies repräsentieren, welche sich chromosomal deutlich von den Individuen mit 2 n = 38 abhebt, die in Ägypten und im Sudan zu finden sind und dem echten *Gerbillus pyramidum* entsprechen. Nach unseren Ergebnissen schlagen wir vor, daß die von Senegal bis Lybien gefundenen Exemplare mit 2 n = 40 einer einzigen Art entsprechen, welche den Namen *Gerbillus tarabuli* tragen sollte. Diese, im nördlichen Afrika weitverbreitete Art zeigt ein anscheinend breites Spektrum an biometrischer Variabilität, die mit der Variabilität des Lebensraums zu tun haben könnte.

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